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Review

Assessment of the impacts of climate change on Mediterranean terrestrial ecosystems based on data from field experiments and long-term monitored field gradients in Catalonia☆

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ABSTRACT

Climate change is increasing temperatures globally and drought in many regions. If climate change continues at its current rate, the resilience of many ecosystems will likely be exceeded, altering their structure and function. A consistent understanding of the impacts, however, remains elusive due to the difficulty of obtaining data of field studies at different scales from local to regional. We review the impacts of climate change on terrestrial ecosystems of the Mediterranean region based mostly on long-term field experiments of climatic manipulation and monitored field sites in Catalonia (NE Spain). These studies provide diverse experimental and observational field evidences that rising temperatures, new patterns of precipitation and other climatic changes are already affecting ecosystems in this Mediterranean region. Rapid genetic, epigenetic and metabolomics changes in plants have been described. They have resulted in changes in morphology, physiology, growth, reproduction, and mortality. Some species are more vulnerable to these changes than others are, which has altered their competitive ability and thereby changed microbial, plant and animal community composition. Many other impacts have been observed in response to climate change, for example an increase in the emission of biogenic volatile organic compounds or an increased risk of fire and a decrease in the absorption of CO_2 in periods of drought. A reduction of the capacity to retain nutrients and C in vegetation is accompanied, in the short term, by an increase in soil C and nutrient contents due to a decrease in the enzymatic capacity and mineralization of soil. The projected increase of torrential rainfalls introduces a scenario of uncertain changes in nutrient cycles, soil fertility and nutrient fluxes at medium and long terms. All these changes in water and nutrient availability suggest, though, net losses in the capacity of Mediterranean forests and shrublands to act as C sinks. Future research should quantify C in above- and belowground biomasses and soils under drought and warming, because this necessary information is lacking. Future studies should also investigate the losses of soil nutrients by leaching and erosion, and the possible feedbacks of land cover changes on water availability and regional climate. Policies of environmental and forestry management should take into account these impacts of the environmental and climatic conditions projected for the coming years and decades.

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1. Introduction

The Mediterranean region, as most regions in the world, is warming and becoming increasingly arid (Penuelas et al., 2005; IPCC, 2013). Precipitation in the Mediterranean region has begun to either decrease in the long term, mainly in the dry season (Esteban-Parra et al., 1998), or not change significantly (Penuelas et al., 2005; Piñol et al., 1998). In all cases, though, an increase in potential evapotranspiration has led to increased aridity (Penuelas et al., 2005; Piñol et al., 1998) since temperatures have also increased in Mediterranean region (Penuelas et al., 2005, 2002; Penuelas and Boada, 2003). This increase of aridity comes together with associated disturbances such as floods, extreme heat and drought events and forest fires all them having strong impacts on many ecosystems (Penuelas et al., 2013). Mediterranean plant communities are generally dominated by sclerophyllous woody plants with an herbaceous or shrubby understory (Specth, 1981; Orshan, 1983). The most specific structural characteristics of Mediterranean plants are those related to conservative mechanisms linked to the avoidance of water stress but frequently also to the scarcity of soil nutrients (Specht, 1981; Sardans and Penuelas, 2013). But, despite the great array of physiological and morphological adaptations of Mediterranean plants to cope with drought and nutrient scarcity (Gulías et al., 2002; Fioretto et al., 2003; Padilla and Pugnaire, 2007; Vilagrosa et al., 2010; Sardans and Penuelas, 2013) a cascade of feed-back effects among increased aridity, more frequent torrential rainfalls and fires, and land-use changes have exceeded the capacity of Mediterranean plants to cope with drought, for instance in several areas of central and south Spain (Moreno-de las Heras et al., 2011; Ruiz-Sinoga et al., 2011, 2012). Most studies suggest a significant positive and rapid feedback between soil properties linked to fertility (water-storing capacity, permeability, nutrient availability, depth) and plant cover (Gallardo et al., 2000; Johnson-Maynard et al., 2002; Castaldi et al., 2009; Ochoa-Hueso et al., 2011). All these processes have further impacts on soil fertility and stability linked to less organic matter inputs, increased photodegradation of litter when plant cover decreases and more erosion associated to torrential rainfalls (Riera et al., 2007; González-Hidalgo et al., 2007; Moreno-de las Heras et al., 2011; Barnes et al., 2012).

All these processes which are temperature- and water-dependent are thus very likely to be altered by climate change. We here have reviewed the available data for the impacts of climate change at different spatial and temporal scales in the Mediterranean region from the long-term monitoring of field studies in Catalonia (NE Spain) highly representative of the terrestrial ecosystems of the Mediterranean region. These long-term field studies include experiments of climatic manipulation (Prades and Garraf), long-term monitored field gradients (e.g. in Montseny) and the Catalan Forest Inventory, all in Mediterranean woodlands (Fig. 1). Some of these data were collected by the authors to report the effects of climate change on the terrestrial ecosystems of Catalonia (Penuelas et al., 2016). The two experimental sites represent two of the most typical terrestrial Mediterranean ecosystems, the semi-arid shrubland and the evergreen forest. The Garraf site has a typical calcareous shrubland representative of the Mediterranean communities with semi-arid conditions with widely distributed Mediterranean shrubs such as *Erica multiflora* or *Globularia alypum*, as dominant species. The evergreen-Quercus ilex forest of Prades mountains represents the Mediterranean mesic climatic ecosystem with *Quercus ilex* as dominant tree. The long-term monitored field gradients of Montseny range from the Mediterranean *Quercus ilex* forest at low altitudinal level to the European wet temperate *Fagus sylvatica* forest in high altitudinal levels.

This study focuses on the reported effects of climate change on the genetics, epigenetics, morphology, physiology and phenology of living organisms; interactions between species; changes in species composition; the structure and functioning of ecosystems; and finally the effects of biological changes on the C and nutrient cycles.

2. Field sites

The Garraf experimental site is a dry shrubland (Rosmarino-Ericion) in Garraf Natural Park, Barcelona, northeastern Spain (41°18′N, 1°49′E), at 210 m a.s.l. and on a south-south-eastern slope (13°). The climate is typically Mediterranean, with a mean annual precipitation of 455 mm and a mean annual temperature of 15.1 °C (Beier et al., 2004). The site, which is located on terraces of abandoned vineyards, was burned in the summers of 1982 and 1994. The soil is a petrocalcic calcixerept, thin (12–37 cm), with a loamy texture and abundant calcareous nodules. The regenerating vegetation currently covers 50–60% and has a maximum height of 70 cm. The dominant species, *Erica multiflora* L. (*Ericaceae)* and *Globularia alypum* L. (*Globulariaceae*), are evergreen, sclerophyllous shrubs that typically occur on basic soils of the western Mediterranean Basin, where they are common components of the coastal shrubland. Nine 20-m^2 (4 × 5 m) plots were established: three untreated control, three warming and three drought plots. The plots were organized in three blocks (each block with one control, one drought and one warming plot). Control plots had scaffolding similar to the warming and drought plots, but with no curtains to exclude rain or retain heat (see below). All plots were open around their edges. The outer 0.5 m of each plot was considered a buffer zone, and all measurements were conducted in the central 12 m^2.

We established two types of climatic manipulation using automatically sliding curtains (approx. 20 cm above the maximum height of the vegetation). (1) Extended summer drought was induced by covering the natural vegetation and soil with transparent and water-proof plastic curtains during all rains over two growing seasons, from March–April to July–August and from September–October to December–January. Rain sensors closed the curtains in the drought treatment to cover the plants and soil during a rain and opened them when the rain stopped. (2) Passive night-time warming was achieved by covering the vegetation and soil at night with aluminum curtains. Solar energy accumulates in the ecosystem during the day, and a fraction of the energy is re-radiated back to the atmosphere at night as long-wave infrared radiation. The covering of the ecosystem with the curtains at night reduced the loss of infrared radiation, simulating the mechanism of global warming from the accumulation of greenhouse gases. The coverage of the plots was activated automatically by a preset light level ($< 5\ \mu mol\ m^2\ s^1$). This treatment began on 16 March 1999 and continued throughout the study, except during three periods (August 1999, January 2000 and September–October 2001), when the treatment was stopped for calibration of the system effects or due to mechanical problems. The curtains were automatically opened during night-time rains to avoid excluding precipitation. For more detailed information, see (Beier et al., 2004).

The Prades experimental site was established in 1998 at the Prades holm-oak forest in southern Catalonia (northeastern Iberian Peninsula) (41°21′N, 1°20′E) at 930 m a.s.l. on a south-facing slope (25% slope). The forest is dominated by holm oak (*Quercus ilex*) and the tall shrubs *Phillyrea latifolia* and *Arbutus unedo*. The forest has a very dense multistem crown (18 366 stems ha^{-1}), with 3850 stems ha^{-1} and 50 Mg ha^{-1}, 12 683 stems ha^{-1} and 29 Mg ha^{-1} and 667 stems ha^{-1} and 9 Mg ha^{-1} of *Q. ilex*, *P. latifolia* and *A. unedo*, respectively. These three species are accompanied by other Mediterranean woody species that do not reach the upper canopy (e.g. *Erica arborea* L., *Juniperus oxycedrus* L. and *Cistus albidus* L.) and the occasional isolated deciduous tree (e.g. *Sorbus torminalis* L. Crantz and *Acer monspessulanum* L.). This forest has been managed as a coppice for centuries but has not been substantially disturbed in the last 70 years. The climate is typically Mediterranean. The site has had a mean annual precipitation of 610 mm and a mean annual temperature of 12.2 °C since the beginning of 1998. The annual and seasonal distribution of precipitation is irregular, with annual precipitation ranging from 376 to 926 mm in the 12 years of the experiment described below. Spring and autumn are the wettest seasons, and summer droughts usually last three months, during which

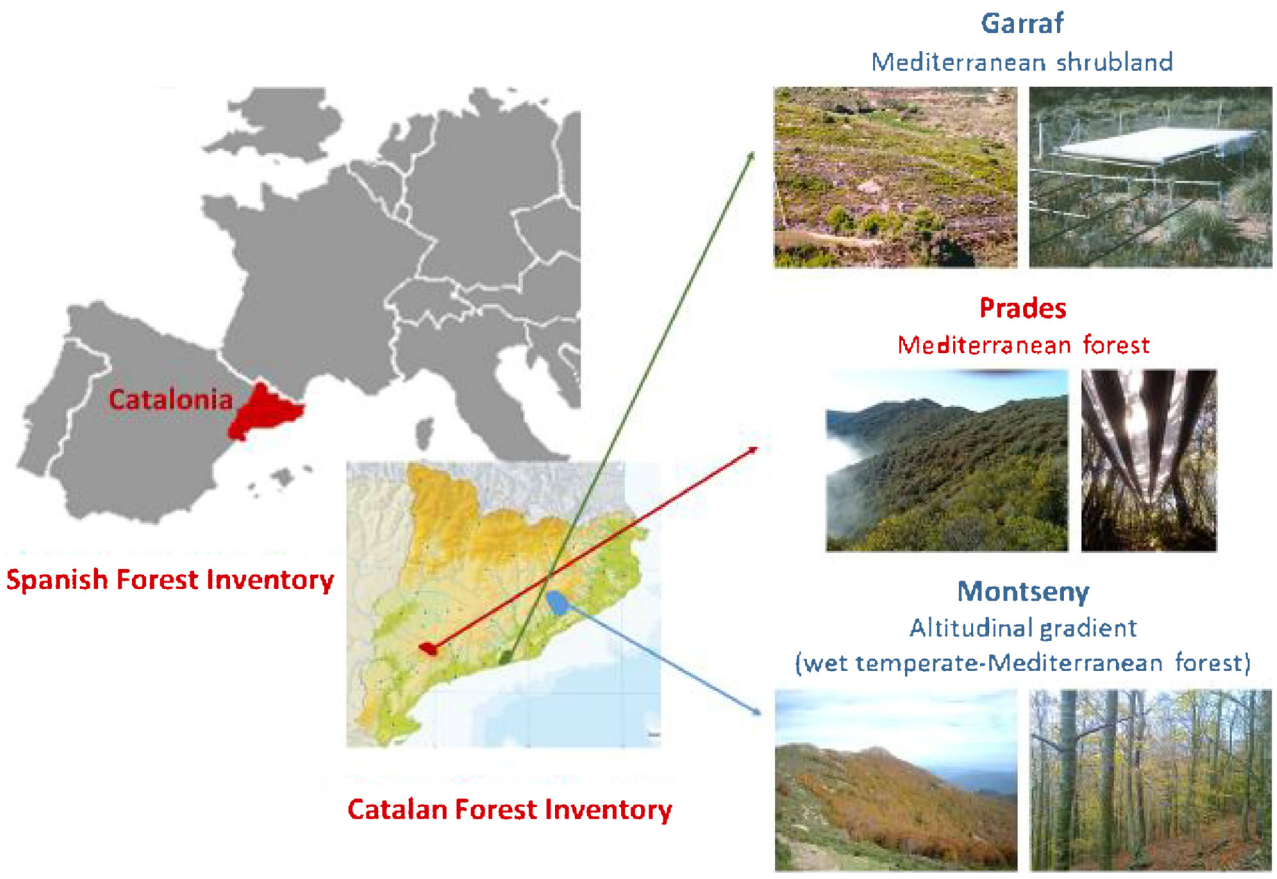

Fig. 1. Catalan experimental and long-term monitorin field sites of the study. Spanish and Catalan Forest Inventories were also used in this study.

precipitation is ~10% of the annual total and coincides with the highest temperatures. Winters are relatively cold. January is the coldest month (mean temperature of 4.4 °C), and the mean daily temperature is < 0 °C an average of eight days per winter. The soil is a Dystric Cambisol over Paleozoic schist and has a mean depth of ~35 cm. The mean annual precipitation is higher than that in the driest distributional limit of *Q. ilex*, but the topographic characteristics of the study site represent drier conditions due to the shallow soils and steep terrain.

The experimental system consisted of eight 150-m^2 plots delimited at the same altitude along the slope. Half the plots (randomly selected) received a drought treatment, and the other half faced natural conditions. Precipitation was partially excluded from the plots of the drought treatment by PVC strips suspended 0.5–0.8 m above the soil and covering approximately 30% of the plot surfaces. A ditch 0.8 m in depth was excavated along the entire top edge of the plots to intercept runoff water. The water intercepted by the strips and ditches was conducted around the plots, below their bottom edges. The strips were installed below the canopy and thus did not intercept direct sunlight. Litter falling on the plastic strips was regularly transferred below them to ensure that differences in the content of soil nutrients among treatments and control plots were attributable only to the availability of water for the decomposition of this litter. For more details, see Ogaya and Penuelas, (2004).

The holm-oak and beech forests in Montseny Natural Park have been monitored since 2002. The studies were conducted in the northeast of the Iberian Peninsula, at the southern edge of the distribution of *Fagus sylvatica* in Europe (Jump et al., 2006a,b; Penuelas and Boada, 2003; Penuelas et al., 2007). The holm oak and beech forests in the park are 50 km northeast of Barcelona (Catalonia) (41°42′-41°52′N, 2°16′-2°33′E). Beech colonized the Montseny Mountains more than 4000 years ago (Comps et al., 2001). The northeastern ridge of the Montseny Mountains rises to 1712 m a.s.l. and includes 2380 ha of nearly continuous beech forest (Jump et al., 2006a). The southwestern ridge rises to 1344 m a.s.l. and is mainly dominated by pastures that occupy the top of a high plain, and fragments of beech forest are restricted to the steeper surrounding areas. Individual fragments cover an area of up to 52 ha (Jump and Penuelas, 2006) (Fig. 1). The two ridges are separated by a valley, so the fragments and continuous forests are separated by 1.5–5.5 km. Beech forests occur above 1000 m a.s.l. and form the tree line on the highest peaks of the region (Turó de l'Home and Les Agudes, 1712 and 1706 m, respectively). The vegetation below the beech forest in all areas of these mountains is Mediterranean, dominated by *Q. ilex* (Penuelas et al., 2007). The bedrock consists mostly of metamorphic phyllites and schists (Àvila et al., 2002; Comps et al., 2001), with some areas of granodiorites on the northeastern ridge.

We have also used the data from the inventory of the Catalan National Forest (Gracia et al., 2004) to analyze the relationships of the climatic gradients of this region with forest traits and to test different scenarios using the program GOTILWA (Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2014, 2017) to project future conditions for Mediterranean forests.

3. Responses at the molecular level and the use of elements: genetics, epigenetics, metabolomics and stoichiometry

The interaction of genetic variability in natural populations with climate induces the emergence of adaptive and evolutionary responses to new climatic conditions. The application of various techniques of molecular biology to the study of natural forest populations has allowed the identification of loci associated with these responses to climate, quantifying their frequency in the population and determining the role of genetic modifications in a fast adaptive response. Field studies of altitudinal gradients in the Montseny Mountains (Jump et al., 2006a,b; Jump and Penuelas, 2006) and field-warming and drought-

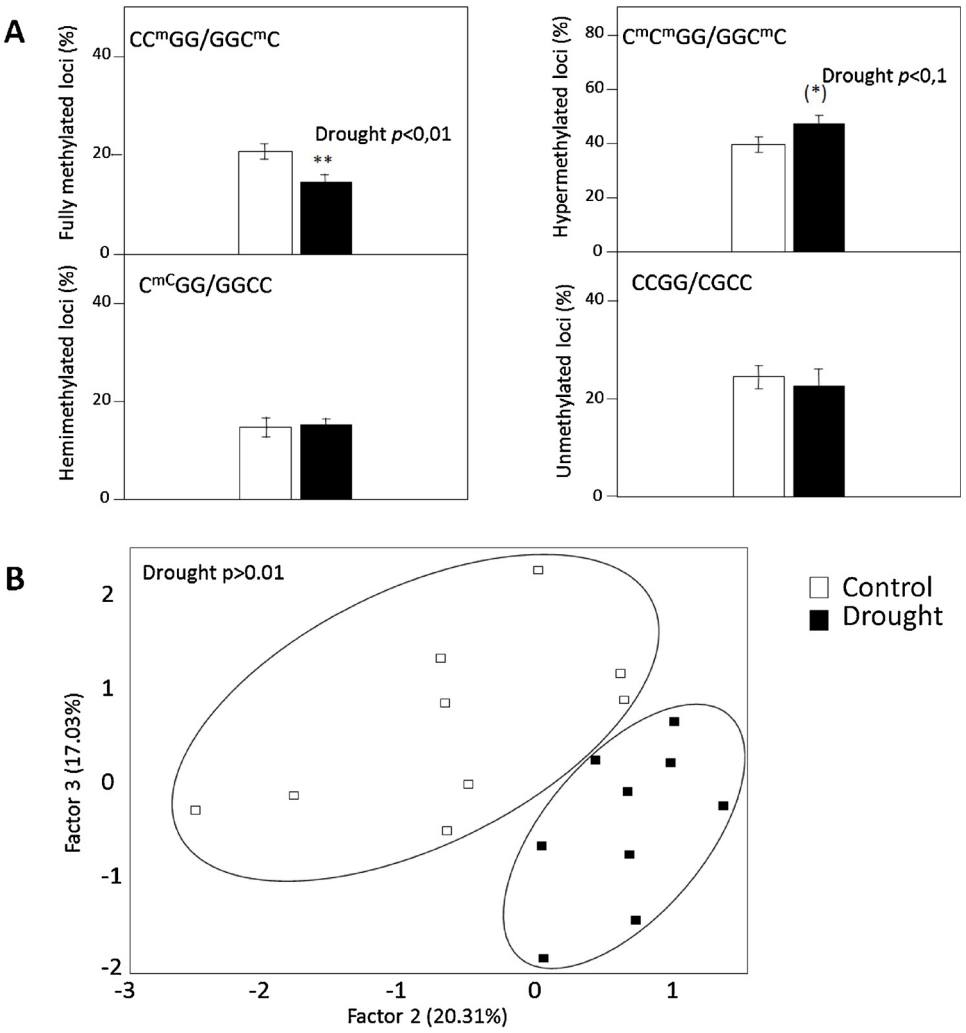

Fig. 2. Epigenetic study of natural populations of *Quercus ilex* under control and drought conditions. A) Patterns of methylation of spot samples showing the percentages (mean ± SE) of each state of methylation of the GGCC sequence analyzed. The differences were analyzed by an ANOVA. *, $P < 0.1$; **, $P < 0.01$. B) Principal component analysis of methylation at each type of locus in populations of *Q. ilex*. The percentages indicate the proportion of variance explained by each factor. The effect of the drought on factors 2 and 3 have been calculated using an ANOVA. For more details, see Rico et al. (2014).

manipulation experiments in typical Mediterranean shrubland in the Garraf Mountains (Jump et al., 2008) have demonstrated rapid responses for the acclimation and adaptation (evolution) of species to climate change by taking advantage of the existing genetic variability in natural populations.

Genetic changes have thus been detected in the response of plants to progressive drought and warming, but alterations in gene expression not attributable to variations in DNA sequences have also been detected. These epigenetic changes can occur in complex and interrelated molecular processes, such as DNA methylation, histone modification and RNA regulation. DNA methylation is stable over time at the individual level, has varying degrees of heritability and may be influenced by the environment. The ability of tree species to respond quickly in natural conditions by epigenetic changes, such as those observed in *Q. ilex* subjected to experimentally induced drought, were determined using specific molecular markers sensitive to DNA methylation (Rico et al., 2014) (Fig. 2).

Metabolomic analyses of wild plants have identified decreases in the activity of the metabolic pathways associated with the accumulation of energy and growth and increases in the activity of secondary metabolic pathways associated with anti-stress mechanisms in response to drought in dominant species of Mediterranean shrubs and trees (Rivas-Ubach et al., 2016, 2014, 2012). Field experiments of climate manipulation have shown changes in elemental composition (Sardans et al., 2013). Moreover, the changes in elemental composition are linked with the functional shifts of plants under higher levels of drought and warming as observed in metabolomic studies (Rivas-Ubach et al., 2016, 2012). These effects of climate change on leaf elemental composition have shown to be associated with the level of herbivore pressure suggesting shifts in leaf palatability (Rivas-Ubach et al., 2014). Differences in soil depth are also directly associated with the metabolomic structure of trees, indicating that droughts can more significantly affect trees in shallower soils (Rivas-Ubach et al., 2016). Moreover, warming and drought can affect chemical composition of aerial plant organs differently and even oppositely than roots (Gargallo-Garriga et al., 2015, 2014) (Fig. 3). A decrease in activity of the metabolic pathways in primary metabolism associated with growth and decreases in N, P and K concentrations have been observed in the aerial organs. In contrast, higher concentrations of N, P and K and of primary metabolites involved in protein synthesis and energy production, such as amino acids and sugars, have been found in roots. These assymmetrical effects on above- versus belowground chemical composition can also have asymmetrical and/or different consequences in above- versus belowground trophic webs.

Field experiments of warming and drought have een thus associated to changes in elemental composition (Sardans et al., 2013, 2012b). Changes in elemental composition and stoichiometry are linked to shifts in the flow of matter and nutrients through the trophic chain and therefore modifications of the biogeochemical cycles of the plant-soil system (Sardans et al., 2012c; Sterner and Elser, 2002). Foliar C/N/P/K stoichiometric ratios of the main forest species in studies of climatic gradients were largely due to weather conditions, especially rainfall (Sardans et al., 2016, 2015, 2011; Sardans and Penuelas, 2014, 2013a,b). This relationship has also been observed in the same species

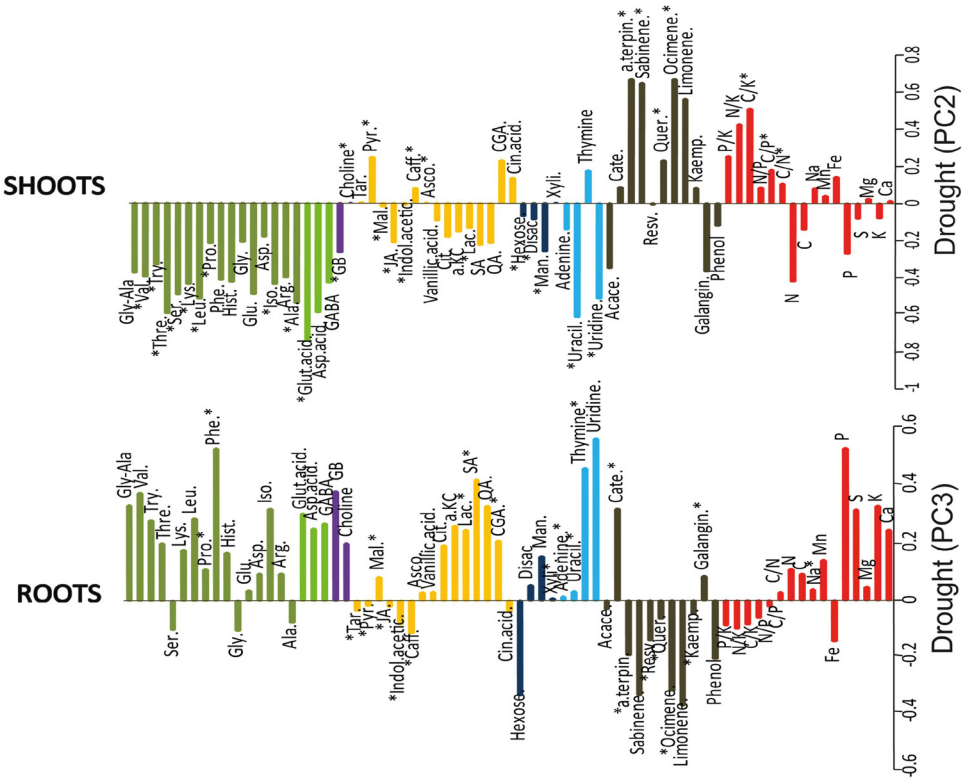

Fig. 3. Metabolome of shoots and roots in response to drought Shoots are metabolically deactivated during drought to reduce the consumption of water and nutrients, whereas roots are metabolically activated to enhance the uptake of water and nutrients, together buffering the effects of drought, at least at the short term. The experiment was conducted with a common grass species, *Holcus lanatus* L., submitted to drought conditions in the field.The various metabolomic families are represented by colors: blue, sugars; green, amino acids; dark green, amino-acid derivatives; yellow, compounds associated with amino-acid and sugar metabolism; cyan, nucleotides; violet, osmolytes and brown, terpenes and phenols. Metabolites: glycine-alanine (Gly-Ala), valine (Val), tryptophan (Try), threonine (Thr), serine (Ser), lysine (Lys), leucine (Leu), proline (Pro), phenylalanine (Phe), histidine (Hys), glycine (Gly), glutamine (Gln), asparagine (Asn), isoleucine (Ile), arginine (Arg), alanine (Ala), glutamic acid (Glu), aspartic acid (Asp), gamma-aminobutyric acid (GABA), glycine betaine (GB), choline (Choline), tartaric acid (Tar), pyruvate (Pyr), malic acid (Mal), jasmonic acid (JA), indol acetic acid (Indol.acetic), caffeic acid (Caff), ascorbic acid (Asco), vanillic acid (Vanillic.acid), citric acid (Cit), α-ketoglutaric acid (αKC), lactic acid (Lac), shikimic acid (SA), quinic acid (QA), chlorogenic acid (CGA), chinic acid (Cin.acid;), xylose (Xyli), hexose (Hexose), mannose (Man), disaccharides (Disac), adenine (Adenine), uracil (Uracil), thymine (Thymine), uridine (Uridine), acacetin (Acace), catechin (Cate), α-terpinene (αTerpin,), sabinene (Sabinene), resveratrol (Resv), quercetin (Quer), ocimene (Ocimene), limonene (Limonene), galangin (Galangin), kaempferol (Kamp) and phenolic groups (Phenol).For more details, see Gargallo-Garriga et al. (2014).

across its distributional area rainfall (Sardans et al., 2016). Decreases in water availability are therefore associated with shifts in nutrient concentrations and their allocation to different organs (Sardans and Penuelas, 2013a,b), the stoichiometric relationships among the main nutrients (Sardans et al., 2008a,c; Sardans and Penuelas, 2013a,b) and the distribution of nutrients between plants and soils (Sardans et al., 2008a,c,d).

4. Morphological, physiological, phenological and growth changes in plants

All metabolic responses mentioned above have a strong effect on the growth and development of organisms in the medium and long term. For example, a small reduction in soil moisture in Prades has significantly reduced the biomass increases in holm oaks (Barbeta et al., 2013; Liu et al., 2015; Ogaya and Penuelas, 2007a). This strong decrease in the growth of trees has been produced by both a slight decrease in net photosynthetic rates and an increase in defoliation (Ogaya and Penuelas, 2004). High mortality rates have also been observed in the last two decades due to periods of extreme drought (Ogaya et al., 2015). These negative effects, however, have progressively decreased, probably due to epigenetic adaptation, a decrease in foliar biomass and/or unknown reasons (Liu et al., 2015). The effect of drought, however, can finally increase over time by the exhaustion of deep soil water (Barbeta et al., 2015).

Our field study sites at Prades and Garraf have allowed us to observe the sensitivity of Mediterranean species to severe warming and drought conditions despite their strong ability to acclimate to warm and dry conditions (Llorens et al., 2004; Munné-Bosch et al., 2004; Munné-Bosch and Penuelas, 2004; Sardans and Penuelas, 2013b; Serrano et al., 2005). The experimentally induced drought in Prades delayed the phenophases of leaf shedding and flushing, flowering and fruit growth, manipulation and abscission in A. unedo but not those of the two other dominant species, *Q. ilex* and *P. latifolia* (Ogaya and Penuelas, 2004). It decreased the growth and increased the mortality of *Q. ilex* and A.unedo (Barbeta and Penuelas, 2016; Barbeta et al., 2013; Ogaya and Penuelas, 2007a). These results thus showed that a drought-resistant species such as *P. latifolia* could have a greater ability to grow and produce reproductive structures than less resistant species such as *Q. ilex* or A. unedo in a drier environment, as predicted for Mediterranean areas in the near future by models of global circulation.The Garraf experiment produced similar results; drought and warming had negative effects on flower production in some shrub species but not others (del Cacho et al., 2013b). In contrast, flower production was reduced in the drought and warming treatments in the spring-flowering species *Dorycnium pentaphyllum* and *Helianthemum syriacum* but not in the autumn/winter-flowering species *E. multiflora*, which increased flowering in the warming treatment (del Cacho et al., 2013b). Seedling emergence in two of the dominant species in these shrublands, *E. multiflora* and *G. alypum*, decreased significantly in the drought treatment, and the decrease was larger in open areas than below vegetation cover. Seedling survival for both species decreased closer to competing neighbors, and survival in *G. alypum* was higher with lower mean annual temperatures and higher annual rainfall, but survival was also higher in the drought treatment, where vegetation cover decreased (del Cacho et al., 2013a). This study supports the prediction that the increasing aridity in Mediterranean ecosystems would constrain the early stages of development in typical co-occurring shrubs. Both field studies thus suggested that these different responses among species for some variables contributing to reproductive success could produce changes in seedling recruitment and resprouting ability and, in the longer term, in species distribution.

Drought increases terpene emissions of holm oak forests in Prades mountains, specially in more biologically active seasons, spring and autumn (Llusià et al., 2006; Llusia and Penuelas, 2000), with large differences among species (Llusià et al., 2008, 2006). Terpene emissions have also increased in three of the four species in the drought treatment at the Garraf experimental site (Llusià et al., 2008). These shifts in plant terpene contents and emissions have a great significance for the fire

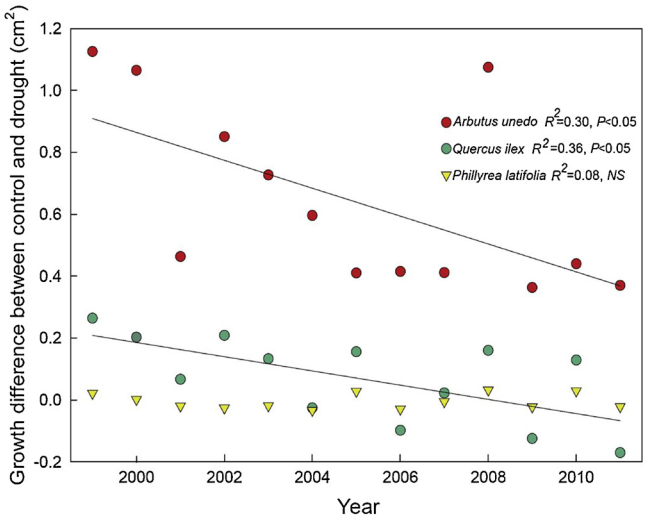

Fig. 4. Differences in basal-area growth between the control and droughted plots in the field experiment in the Prades Mountains for three species (*Arbutus unedo, Quercus ilex* and *Phillyrea latifolia*). The coefficient of determination and the significance level of the temporal trend of the dependent variable for each species are indicated. [For more details, see Liu et al. (2015) and Barbeta et al. (2013)].

patterns due to the great importance of terpenes in the flamability of forests (Alessio et al., 2008a,b).

5. Changes in populations and communities

Our climatic-manipulation field experiments have demonstrated that prolonged drought drives asymmetrical changes in species populations, with some species more negatively affected than others (Barbeta et al., 2013; Prieto et al., 2009). These results highlight the variable vulnerability of Mediterranean species to more frequent and intense droughts, which may lead to partial species substitution and changes in forest structure and thus C uptake. The response to drought, however, changed over time. Decreased intra- and interspecific competition after extreme droughts with high mortality, together with probable morphological and physiological acclimation to drought during the study period, may buffer forests against drier conditions, at least in the short term. The species-specific responses to drought may eventually lead to a partial communal shift favoring the more drought-resistant species. The effect of the drought treatment, however, was dampened for the two drought-sensitive species after 13 years in the Prades experiment, which may indicate a potential adaptation to drier conditions at the ecosystemic or populational level (Barbeta et al., 2013). The effect of drought treatment also differed among species in the post-fire Mediterranean shrubland in the Garraf experiment. The drought and warming treatment reduced the competitive ability of the obligate seeder tree *Pinus halepensis* against native resprouter shrubs, which slowed the transformation of the dominatant vegetation from shrubs to pine trees. Conversely, the strategy of water use by *G. alypum* may have allowed this species to maintain a dominant position in the drought plots (Prieto et al., 2009).

A metadata analysis found that the different responses of each individual and species to climate change generated both demographic changes and changes in the composition and functioning of the communities, consistent with the results at the experimental field sites (Carnicer et al., 2013a,b). Gymnosperms are currently been replaced by Quercus sp. in several areas of the Iberian Peninsula due to their different roles during succession and basic traits (Carnicer et al., 2014). On the other hand, the most representative *Quercus* tree species in Mediterranean basin, *Q. ilex*, is suffering decreases of growth and increased of mortality and defoliation (Penuelas et al., 2000, 1998). Moreover, in the same areas tall shrubs better adapted to arid environment than trees are minimally affected by drought (Liu et al., 2015; Penuelas et al., 2000, 1998), suggesting that if climate becomes drier the in Mediterranean Basin the trend towards a replacement of trees by tall shrubs could become stronger.

6. Disturbed communities and young ecosystems are the most sensitive

Changes in the abundance and dominance of species were monitored by Kröel-Dulay et al. (2015) in a long-term experiment (14 years) simulating warming and drought growing conditions in seven shrubland ecosystems geographically distributed throughout Europe. The study included sites that had not been disturbed for a long time and others that had suffered recent fire or pests, as was the case of the fire in the Garraf Mountains (Barcelona) in 1994. The ecosystems that had been altered, either by natural causes or human activity, were most vulnerable to climate change (Kröel-Dulay et al., 2015). The association between human activity and the frequency and severity of disturbances that disturb ecosystems suggest that disturbed ecosystems will respond more strongly to climate change. These studies demonstrate the need to know the history and successional state of ecosystems for accurately predicting their responses to climate change, paying special attention to recently degraded ecosystems currently in early successional stages.

7. Biogeochemistry and ecosystemic functioning

7.1. Responses of the holm-oak forests to long-term drought

The drought experiments in the forests indicated that an increase in the intensity, frequency and duration of droughts can negatively affect Mediterranean ecosystems, such as those of *Q. ilex* forests (Carnicer et al., 2011). If water availability decreases, trees transpire less, assimilate less C and thus grow less. In addition, an increase in mortality in the species more vulnerable to drought could favor the more resistant species, thereby changing the structure and composition of ecosystems and the environmental services they offer. Differences in the rates of growth recorded between drought and control plots at the beginning of an experiment in Prades between 1999 and 2011, however, eventually decreased or disappeared (Fig. 4) (Barbeta et al., 2013; Liu et al., 2015). The causes of the dampening effect of drought are several but could be partly result of the reduction in competition for water resources between individuals due to the death of more individuals in the drought than the control plots. This compensation of the effect of drought treatment was also accelerated by episodes of extreme drought, such as the drought during 2005 and 2006 that dramatically increased mortality. Adjustments in the morphology, allometry and physiology of trees from epigenetic modifications may have also contributed to the acclimation of the forest to drier environmental conditions (Barbeta et al., 2013).

The drought treatment in the Prades experiment reduced flower and fruit production in *Q. ilex* by 30 and 45%, respectively, whereas these variables did not change significantly in the other two dominant species, *P. latifolia* and *A. unedo* (Ogaya and Penuelas, 2007b). The decreases in growth and fruit production in some species, despite being asymmetrical among species, was nevertheless accompanied by a global decrease of biomass in the plant community.

Mushrooms have also decreased production in response to drought (Ogaya and Penuelas, 2005), all of which strongly suggest a slow shift from a mesic evergreen oak forest to a drier forest with increasing relative dominance of the tall shrubland *P. latifolia*, the species that has generally been damaged less by the 17 years of experimental drought in the Prades Mountains.

The use of stable isotopes indicated that the deep soil water was the preferred usage during summers, and water from surface horizons was preferentially used in wet seasons. The drought treatment plots in our drought-manipulation field studies, however, did not follow this

pattern; the trees took up more deep water in the wet seasons (Barbeta et al., 2015). This difference may have been due to differences in the distribution of fine roots, which extended to greater depths in the drought plots to avoid summer dessication. The experimentally induced drought instead decreased the use of this deeper water in the summer, probably due to the depletion of the water trapped in rock fractures (Barbeta et al., 2015).

These studies mainly indicated that the resilience of holm-oak forests to an increase in drought is more important than initially thought, so these ecosystems may adapt to a progressive increase of arid conditions. The mechanisms of resistance and resilience to drought at the tree level, however, may not be sufficient to mitigate the effects of extreme episodes of drought and warming (Penuelas et al., 2001). Studies that directly evaluate the consequences of these episodes to the structure and function of ecosystems and to the subsequent recovery and accumulated effect of more than one episode are thus clearly warranted.

7.2. Alterations in the use of nutrients

Recent studies based on data from the Catalan Forest Inventory found that nutrient contents and allocation to different organs (leaves and wood) were significantly correlated with weather conditions and especially with annual precipitation, with higher contents with higher precipitation, especially in the leaves (Sardans et al., 2012a, 2011; Sardans and Penuelas, 2014, 2013a). These results also indicate the importance of the availability of water in our forest ecosystems and how small decreases in the availability of water can have disproportionately large impacts on the ability of forests to retain and accumulate nutrients.

Our experimental studies of climate change simulated under field conditions found that a moderate increase in drought (15–20% decrease in the availability of soil water) generally decreased the concentrations and contents of N, P and micronutrients in the forests (Sardans et al., 2008a; Sardans and Penuelas, 2007). The total content of nutrients in aboveground biomass thus decreased with these levels of drought (Sardans et al., 2006, 2008a,b,d), except for K that increased in the aerial organs of some species (Sardans and Penuelas, 2007). Aridity increased the C:N and C:P ratios of our fields and forests, associated with conservative strategies to adapt to the lower availability of water, with a corresponding increase in sclerophylly (Sardans et al., 2006). Similarly, drought also changed the allocation of nutrients to the organs, increasing the allocation of N to the roots, probably to help fulfil the increased need for water (Sardans et al., 2008b).

Some of the dominant species at our experimental sites in Prades and Garraf had higher foliar K concentrations and K:P ratios and lower C:K and N:K ratios after 11 years of continuous drought (Egilla et al., 2005; Laus et al., 2011; Sardans et al., 2012a). These results are consistent with the tissue concentrations of K for controlling the loss of water from leaves (Babita et al., 2010) by their positive effects on stomatal function (Khosravifar et al., 2008) and the control of osmosis (Babita et al., 2010; Laus et al., 2011). K is especially important in dry environments due to its role in the control of water retention. K can have a significantly positive effect on plant drought resistance in both natural ecosystems (Egilla et al., 2005) and crops (Stone and Moreira, 1996). The use and remobilization of K in Mediterranean plants is associated with the requirements of osmotic control (Milla et al., 2005). A reduction in the availability of K in *Pinus pinaster* in natural ecosystems in the Iberian Peninsula led to an increase in stomatal conductance and consequently a reduction in water-use efficiency (Fernández et al., 2006). Rivas-Ubach et al. (2012) reported increases in foliar K concentrations in *E. multiflora* in summer (the driest period) due to metabolomic shifts toward increasing concentrations of metabolites associated with osmotic control. Analyses of the Catalan Forest Inventory have provided evidence that Mediterranean forests have higher foliar K concentrations in summer, coinciding with drought periods (Sardans et al., 2012a). The changes in plant K concentrations and ratios with N and P in response to drought merits further research for obtaining a better understanding of the relationships between terrestrial plant stoichiometry and environmental changes.

Increases in drought also strongly affect soils, which is critical because soils are main C sinks. Our experiments simulating climate change at a field scale have indicated that the mineralization of organic matter in Mediterranean soils is strongly affected by changes in water availability (Sardans et al., 2012b, 2006; Sardans and Penuelas, 2010, 2005). Soil respiration and the activities of soil and rhizospheric enzymes have decreased in response to moderate levels of increased drought. The decrease in enzymatic activity was directly correlated with the reduction in water content of the soil (e.g. (Sardans and Penuelas, 2010)). The impact of drought on the growth and ability of plants to accumulate nutrients in biomass, along with the decrease in soil mineralization, would promote the accumulation of nutrients in the soil, which would increase the flow of nutrients to water. The experimental drought treatments in the forests of the Prades Mountains thus decreased the ecosystemic N content because they decreased the total biomass content and increased the loss of N by leaching (Penuelas et al., 2013, 2000).

7.3. The effects of climate change on the C balance

C and N accumulation decreased in the aboveground plant communities at our experimental sites after six years of drought treatment, whereas soil organic C and total N increased, indicating slower rates of C and N mineralization and lower N uptake and C fixation together with a slower turnover of soil C and N (Sardans et al., 2008a,c). These results suggest a slowdown in the turnover of ecosystemic C and a decrease in aboveground C accumulation, but the effect of drier conditions on soil at medium and long terms is not clear. The short-term accumulation of soil organic C could therefore decrease because of the successive reduction in aboveground biomass reducing the input of organic matter to the soil, the increase in leaching due to the reduced plant cover and density and the higher frequency and intensity of torrential rains. Moreover, net photosynthetic rate, stomatal conductance and leaf-water potential decreased with increases in vapor-pressure deficits and decreases in soil moisture in *Q. ilex* and *P. latifolia*, the two co-dominant species of the climatic-manipulation field experiment in the Prades Mountain evergreen forest.

A future drier climate may decrease the C stock of Mediterranean species, and some shrub species highly resistant to drought could gain a competitive advantage over *Q. ilex*, currently the dominant species in this forest (Ogaya et al., 2014). This negative impact of drought on the capacity of Mediterranean ecosystems to accumulate C could be even larger if warming is combined with drought.

8. The future: impact of climate change on mediterranean terrestrial ecosystems predicted for the coming decades. GOTILWA + simulations

We here used the Spanish Forest Inventory to evaluate the response of these various types of Mediterranean forests to climate change by using the GOTILWA model of forest growth (Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2014, 2017; www.creaf.uab.cat/gotilwa/). We used the general circulation model ECHAM4 and the A2 socio-economic scenario (850 ppm of atmospheric CO2 by 2100). Fig. 5A shows the projected GPP and net primary production (NPP) for four periods of the 21st century. GPP progressively increases throughout the century as a result of the expected fertilization effect of the progressive increase in atmospheric CO_2, which is manifested mainly in the forests of northern and northeastern Iberian Peninsula. In contrast, NPP widely tends to decrease. The increase in autotrophic maintenance respiration and the progressive increase in the temperature can deplete carbohydrates and progressively decrease forest biomass (Nadal-Sala et al., in

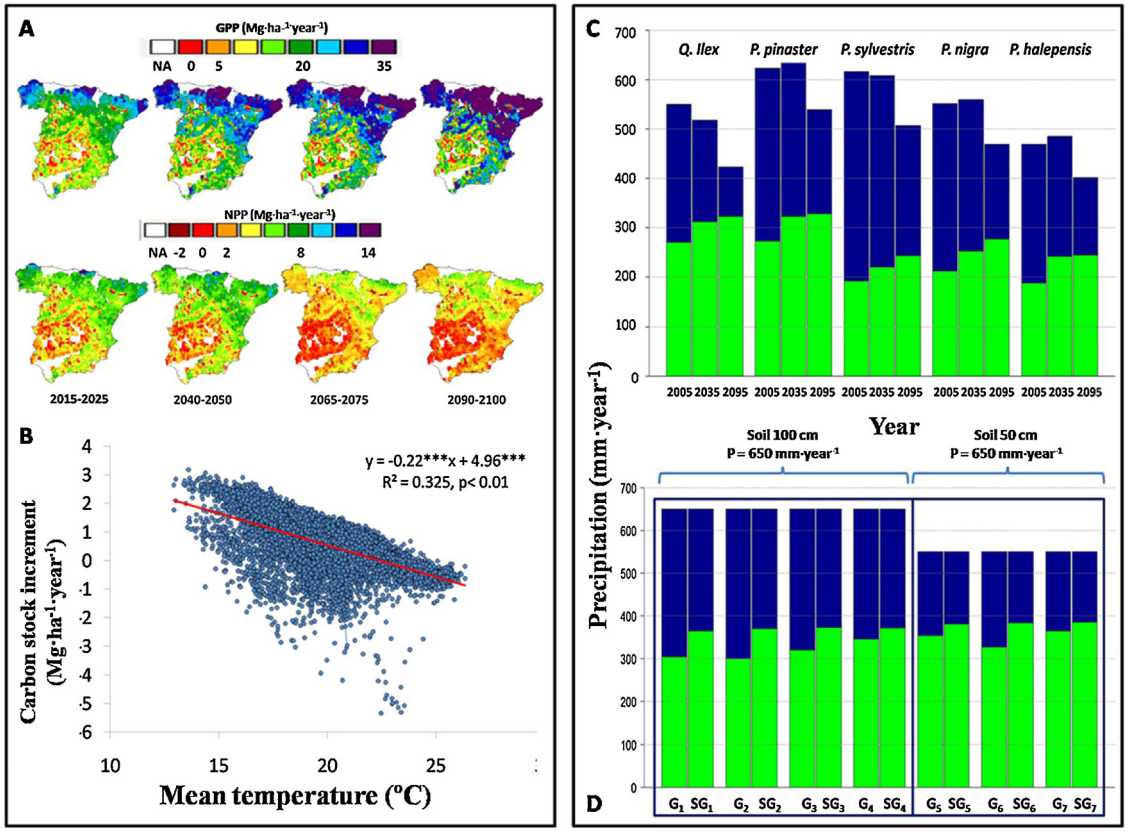

Fig. 5. A) Productivity of mono-specific forests in Spain for socioeconomic scenario A2 (850 ppm of atmospheric CO2 by 2100) and the general circulation model ECHAM4. The number of plots from the Spanish Forest Inventory (IFN) database used in the simulation was 34 000. Upper panels show gross primary production (GPP) and lower panels show net primary production (NPP) by the same stage during four periods of the 21st century. White areas represent where no data were available. B) Increase in forest carbon budged during 2076–2100 period relative to mean annual temperature for the same period. C) Changes in the distribution of blue water (drainage and runoff, blue in the figure) and green water (evapotranspiration, green in the figure) during 21st century. 500 randomly chosen IFN plots in mainland Spain were simulated for the five species noted in the figure. Mean simulated 2000–2010 (2005), 2030–2040 (2035) and 2090–2100 (2095) periods values are represented. Climate change scenario considered was A2 (850 ppm of atmospheric CO2 by 2100) in a ECHAM4 general circulation model (Roeckner et al., 1996). D) GOTILWA+ (Nadal-Sala et al., 2017) simulations of the effects of forest management upon a Pinus halepensis forest water balances in the Montmell Reserve (Catalonia). We analyzed Generalitat de Catalunya's standardized forest management procedures (Beltrán et al., 2011) at increasing turn lengths (turn length G(n) < turn length G(n + 1), minimum turn equals to 47 years, maximum turn equals to 120 years) in two different plot quality conditions (from G1 to G4 correspond to a precipitation of 650 mm y^{-1} and 1 m soil depth forest, and from G5 to G7 correspond to a precipitation of 550 mm y^{-1} and 0.5 m soil depth forest). Each management (Gn) was compared to the corresponding case SG (unmanaged). As in C, D also shows the changes in the distribution of blue water (drainage and runoff, blue in the figure) and green water (evapotranspiration, green in the figure).

press). The loss of biomass is illustrated in Fig. 5B, which shows the negative correlation between the increase in C stocks and air temperature.

The projected increase in temperature and decrease in precipitation simulated by climate-change scenarios also involve a redistribution of green water (evapotranspired water) and blue water (drainage and surface runoff) in the forest types in Fig. 5C. The scenarios predict an increase in evapotranspiration or green water, probably due to the increase in evaporative demand that accompanies higher temperatures. The decrease in precipitation and increase in evapotranspiration, however, would decrease the movement of blue water from the forests to downstream ecosystems. An overall increased water limitation is therefore expected in Mediterranean forests. A decrease in the proportion of the precipitation available for downstream water systems is also expected. Practices of forest management focused on water such as thinning could help to mitigate the growing impact of forests on the green-water fraction. Fig. 5D illustrates various itineraries of forest management, proposed for a *P. halepensis* forest in the Mediterranean region. Forest management could reduce the amount of “green” water, leaving more “blue” water. A decrease in precipitation would decrease the amount of “blue” but not “green” water, which is strictly correlated with evaporative demand in water-stressed environments, such as the simulated *P. halepensis* forests.

9. Final remarks

1. This summary of several studies mainly focused on woody Mediterranean ecosystems, indicates that the projected level of drought and aridity in the next decades may have important effects on the functioning and structure of Mediterranean plants, forests and shrublands. New experimental studies that reproduce natural conditions, including cases of extreme and sudden changes, are needed for better understanding and thus better managing these changes.
2. The experiments at our field sites have provided extensive evidence of the effect of further projected drought increase reducing growth and increasing mortality and defoliation, being this effect asymmetrical between species, thus suggesting a future dominance replacement of trees by tall shrubs.
3. Despite the negative relation between drought and growth, and photosynthesis capacity, Mediterranean species have shown a notable capacity to adapt at short term being this capacity even greater than previously supposed. Epigenetic and genètic processes may have had a key role in this fast capacity of adaptation in some studied species.
4. Drought has a disproportionate effect on nutrient cycle in the plant-soil system. Moderate decreases of soil wàter availability are in general associated to a shift of nutrient from aboveground biomass

to soil, and decrease of mineralization and enzyme activity capacity in soils. The study of the losses of soil nutrients by leaching and erosion should be incorporated into long-term experiments of climatic manipulation in Mediterranean forests. Our studies have provided solid evidence of a trend toward the reduction of aboveground cover and the accumulation of recalcitrant nutrient compounds in soil, suggesting a potential increase in nutrient losses at a higher frequency and/or intensity of torrential rains.

5. Drought has several other impacts such as increases in terpene emissions or accumulation of litter and recalcitrant soil orgànic matter in soil that can further interact with drought and disturbances such as fire and erosion.
6. Future research should quantify accurately the impacts of increasing aridity on the capacity of Mediterranean woodlands to store C in above- and below-ground biomasses and soils, because this necessary information is currently lacking. As it is also lacking the knowledge on the feedbacks of land cover changes on water availability and regional climate.
7. The availlable experimental and observational data provide useful information to improve the Mediterranean forest management in the coming decades. To prevent the increases in mortality, an adequate reduction of the stem density should help to adapt to the aridity rise.

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